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Motion-Sensitive Neurones in V5/MT Modulate Perceived Spatial Position

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Summary

Until recently, it was widely believed that object position and object motion were represented independently in the visual cortex. However, several studies have shown that adaptation to motion produces substantial shifts in the perceived position of subsequently viewed stationary objects [1–3]. Two stages of motion adaptation have been proposed: an initial stage at the level of V1 and a secondary stage thought to be located in V5/MT [4]. Indeed, selective adaptation can be demonstrated at each of these levels of motion analysis [5, 6]. What remains unknown is which of these cortical sites are involved in modulating the positional representation of subsequently viewed objects. To answer this question directly, we disrupted cortical activity by using transcranial magnetic stimulation (TMS) immediately after motion adaptation. When TMS was delivered to V5/MT after motion adaptation, the perceived offset of the test stimulus was greatly reduced. In marked contrast, TMS of V1 had no effect on the changes that normally occur in perceived position after motion adaptation. This result demonstrates that the anatomical locus at which motion and positional information interact is area V5/MT rather than V1/V2.

Results and Discussion

Figure 1 shows a schematic representation of the stimulus arrangement. Subjects adapted to two Gabor patches in which the carrier gratings drifted in opposite directions. This was followed by a brief presentation of two stationary Gabor patches at the same retinal location, and the subjects' task was to judge the position of the upper patch relative to the lower. The perceived offset of the static test stimulus was established after motion adaptation both with and without TMS. The TMS conditions were designed to disrupt the neural consequences of motion adaptation and involved stimulation of V1, right V5/MT, and left V5/MT. After motion adaptation, all four subjects showed a substantial baseline shift, of the order of 8–10 arcmin, in the spatial position of subsequently presented static targets (Figure 2, "baseline condition"). The physical offset of the test stimuli required to produce perceived alignment was in the same direction as the carrier motion and, therefore, in the opposite direction to the MAE. When TMS was delivered to V5/MT after motion adaptation, the perceived offset of the test stimulus was reduced in all four subjects by between 32% and 63%, regardless of the hemisphere stimulated (Figure 1, columns 2 and 3 of each subject's data). In marked contrast, TMS of V1 results in perceived positional shifts that are similar in magnitude to the baseline condition (Figure 1, column 4 of each subject's data). Similar results were obtained for conditions in which the center-to-center separation of adapting and test elements, and the duration of the test phase, was reduced. This indicates that magnetic stimulation of the striate cortex (V1) is ineffective in modulating the changes that normally occur in perceived position after motion adaptation. Thus, it appears that the anatomical locus at which motion and positional information interact is area V5/MT rather than V1/V2.

In a separate control condition, we sought to ensure that the magnitude reduction that occurs in the positional shift when V5/MT is magnetically stimulated was due to an effect on the adapted motion state. We therefore prevented motion adaptation by counter-phasing the adapting stimulus and, once again, delivered TMS to right V5/MT during the test phase. Because no motion adaptation occurs, few or no positional offsets should be present - a finding confirmed for all subjects (Figure 1, column 5 of each subject's data). These data demonstrate that the modulation of positional representation produced by stimulation of the extra-striate cortex (V5/MT) occurs only after direction-selective motion adaptation has taken place.

Prolonged inspection of a moving stimulus has profound consequences on our perception of subsequently viewed objects. For example, the perceived speed, contrast, and direction of subsequent motion can be substantially distorted by prior adaptation [7–9]. This study, along with several other investigations, demonstrates that the positional representation of an object is similarly vulnerable to the influence of motion adaptation, with positional offsets occurring along the axis of real or apparent motion [1–3, 10, 11]. The significance of this finding is that it strongly suggests that the spatial position of an object, or—more accurately—the neural representation of its position, is dynamically updated by neurons involved in the analysis of visual motion. However, the cortical locus at which this interaction between motion and positional information takes place has until now remained elusive. In a previous investigation, we speculated that the spatial characteristics of these motion-induced positional shifts were more in keeping with adaptation occurring at a higher level of motion analysis [2]. In the present experiment we provide prima facie evidence for the involvement of higher motion centers,

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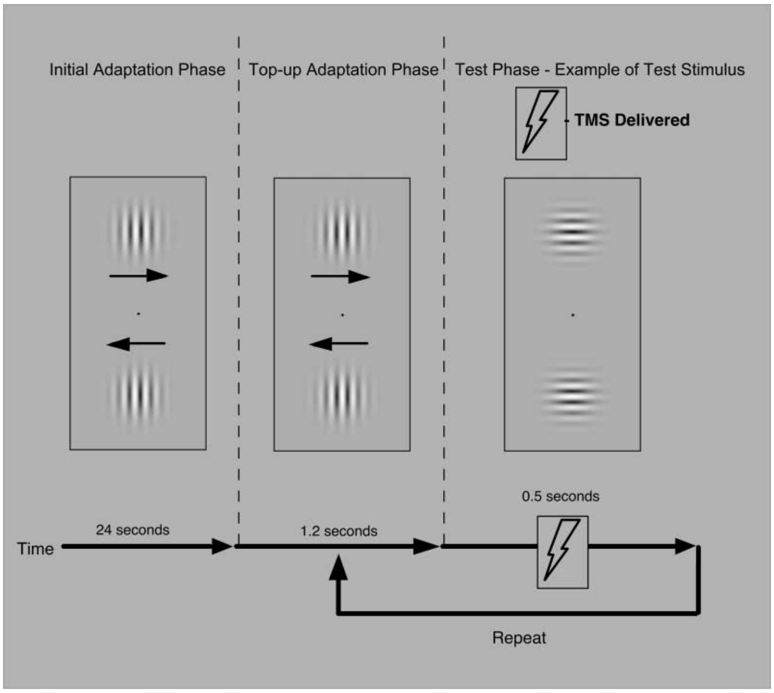

Figure 1. Schematic Representation of the Experimental Setup

The stimulus elements (Gabor patches) consisted of Gaussian-windowed (envelope) sinusoidal luminance modulations (carrier), presented in a vernier alignment test. Prior to the test phase, subjects adapted for 24 s to two stationary Gabor stimuli in which the carrier gratings drifted in opposite directions (contrast of 1; $\sigma = 0.48°$; carrier spatial frequency of 3 cycles/degree; carrier drift velocity of 1.5°/s). After this initial period of adaptation, the adapting stimulus was presented for 1.2 s, followed by the test phase (0.5 s). This cycle of top-ups followed by test phase was repeated until all trials were completed. The elements of the adapting stimulus were spatially coincident with the test elements in the two-blob alignment task. After adaptation, an illusory misalignment of the elements of the test stimulus was perceived, and the magnitude of this perceived offset was established via standard psychophysical procedures. In some conditions, TMS was delivered to striate (V1) and left or right extra-striate (V5/MT) cortex immediately after the adaptation phase and throughout the test phase. TMS was applied in trains of 10 Hz for 0.5 s, at 65% of stimulator output via a Magstim 200 Super-Rapid system with a 70 mm figure-of-eight coil (Magstim, Whitland, UK). Observations were carried out under dim room illumination under monocular viewing conditions (right eye in all subjects). All observers undertook several practice sessions prior to data collection. In two of the subjects, the coil location was coregistered with structural MRI scans; in the other two subjects, the use of stationary and moving phosphenes established the locus of V1 and V5/MT. A full description of the stimuli and TMS localization is available at http://www.brad.ac.uk/acad/optom/staff/PVMcGrawProfile.htm.

specifically area V5/MT, in the visual cortex in the generation of motion-induced positional biases. Cortical disruption of ongoing neural activity in area V5/MT reduces the positional bias normally experienced by human observers after adaptation to unidirectional visual motion. In marked contrast, disruption of lower centers of visual analysis, such as V1, has little or no effect.

Nishida & Johnston [1] have suggested the intriguing possibility that known anatomical connections between V5/MT and lower cortical areas, such as V1 and V2, may form the neural substrate for interactions between motion and positional information. They proposed that the seat of positional judgments lies in lower cortical areas (because the small scale of receptive fields in these areas supports high degrees of positional sensitivity) and that recurrent input from V5/MT continuously updates this representation. Although this scheme would finally ascribe some functional role to the feedback connections known to exist between V5/MT and V1, several lines of evidence make this seem less likely. Although V1 receptive-field properties endow high localization accuracy, the perceptual decision of overall object location is unlikely to be made at this level. Indeed, a recent investigation using functional magnetic resonance imaging (fMRI) and similar visual stimuli to those used in the present study has shown that the retinotopic representation of stimulus position in the primary visual cortex (V1) differs considerably from its perceived location when motion is present [12].

A more parsimonious framework would be for a positional estimate to be available at higher stages of visual analysis, delivered via the normal hierarchical processing structure, and for relevant motion information to exert its influence on perceived location at this later stage. In this situation, the perceptual output might arise from an integration process that considers all available information. Some evidence for such an integration process between motion and perceived position does exist. For example, presenting an area of randomly moving dots simultaneously with adjacent areas of coherently moving dots results in global positional shifts entirely consistent with the degree of integration of dot populations [13]. If the experimental conditions are such that global motion integration takes place, global positional shifts result. Conversely, if integration between coherent and random dot populations is prevented, little or no global shift in position is observed [13]. This result suggests that interactions between motion and positional information occur after the pooling of local motion signals across an extended region of visual space—a property commonly associated with V5/MT. Furthermore, it would appear that information about local features is lost and that instead the influence of motion on relative position is based largely on the motion of perceived surfaces. Other studies also point toward an interaction between motion and positional information occurring at a relatively high level of motion analysis—where perceptual grouping, or integration, of other object attributes such as motion and shape takes place [14].

An interesting finding of the present study is that the reduction in the magnitude of the illusory positional shift following magnetic stimulation of V5/MT is not selective to the stimulated hemisphere. Although there are small inter-subject differences, in general the reduction in off-

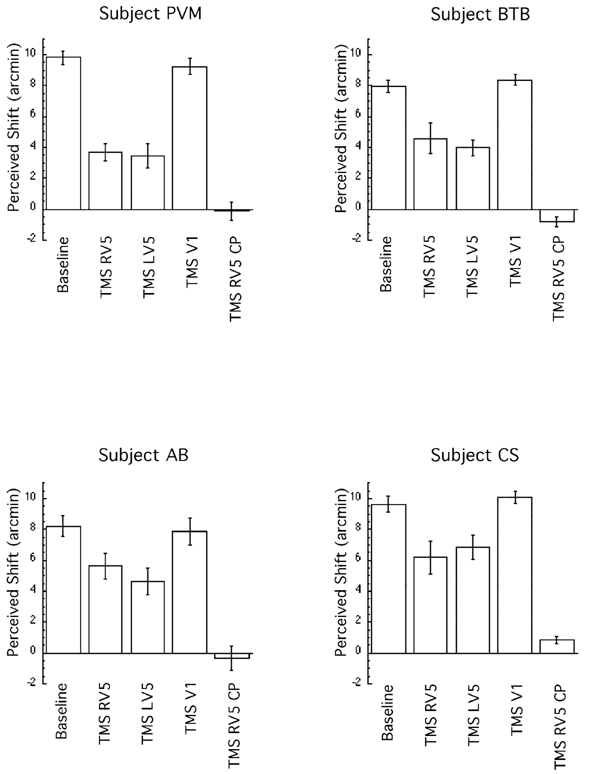

Figure 2. The Magnitude of the Perceived Positional Shifts that Follow Carrier Motion Adaptation

Data are presented for the baseline condition; TMS to right V5/MT; TMS to left V5/MT; TMS to V1; baseline condition with a counter-phasing rather than drifting adapting stimulus; and TMS to RV5 with a counter-phasing rather than drifting adapting stimulus. Error bars represent one standard deviation on either side of the parameter value.

set is surprisingly similar for conditions in which the right V5/MT or left V5/MT is stimulated. Human electrophysiological and brain imaging studies have confirmed the presence of an ipsilateral visual-field representation in human V5/MT. Whereas the retinotopic maps of lower visual areas, such as V1 and V2, extend to the vertical midline, the map of area V5/MT invades the ipsilateral visual field by up to 10°–15° [15, 16]. Therefore, motion in one particular hemifield has the potential to activate V5/MT in both hemispheres. Furthermore, imaging studies in man have revealed that the response to motion in one V5/MT, whether it be ipsilateral or contralateral, is transferred to its counterpart via the spleniuim (posterior part of the corpus callosum), a structure containing neural fibers connecting the occipital lobes [16, 17]. It seems likely that the "neural noise" introduced by magnetic stimulation undergoes a similar information transfer, thus enabling it to exert its influence on both V5/MT areas, regardless of which hemisphere is initially stimulated. In support of this, combined studies of TMS and positron emission topography (PET) have shown that TMS-induced neural activity can be transferred to anatomically connected sites [18].

Although the adapting motion in this particular study is in the fronto-parallel plane, other types of motion, such as motion-in-depth, can also distort the positional representation of static stimuli. Edwards and Badcock [19] have shown that stereoscopic-based judgments are significantly biased by motion either toward or away from an observer. Therefore, our entire three-dimensional representation of visual space is vulnerable to motion-induced perceptual distortions. This, of course, has considerable implications for actions guided by visual information because motion-induced distortions of the positional map could lead to similar errors being translated to the motor system. Whitney and coworkers have recently shown that this is indeed the case [20]. Rapid reaching movements of the hand display systematic errors in the direction of objects moving in the visual field. Perhaps more surprisingly, the visuo-motor system is unable to parse motion information arising from irrelevant objects moving in the background from the static positional information of target objects [20]. There are two possible explanations for this effect. Motion localized to one particular area of the visual field has the potential to distort the positional map over much larger regions of visual space; anything falling within this region, whether it be moving or stationary, may have its location assigned by a common mechanism [21]. Alternatively, the perceptual output may arise from an integration process that considers all available information. Within such a scheme, the contribution of each source of visual information to our final perception may reflect its relative reliability [22]. For example, under conditions where positional certainty is high, motion information may have little or no effect on perceived position. However, with increasing levels of positional uncertainty, estimates of the position of static objects may become increasingly vulnerable to the influence of motion. It remains to be seen whether the magnitude of the positional shift that results from motion adaptation is directly related to the accuracy with which the object can be localized. An answer to this question would shed valuable light on the operational characteristics of the mechanism that integrates motion and positional signals.

In summary, adaptation to motion causes substantial errors in the localization of subsequently presented stationary stimuli. We were able to modulate this effect by disrupting ongoing neural activity in cortical area V5/MT. In contrast, disruption of early visual areas, such as V1, had little effect. We therefore propose that integration of motion and positional information is dependent on extra-striate cortical area V5/MT.

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